Ecosystems (2019) 22: 174–188
https://doi.org/10.1007/s10021-018-0260-2

ECOSYSTEMS
© 2018 Springer Science+Business Media, LLC, part of Springer Nature

Post-fire Redistribution of Soil Carbon and Nitrogen at a Grassland–Shrubland Ecotone

Guan Wang,[1]* Junran Li,[1] Sujith Ravi,[2] David Dukes,[2] Howell B. Gonzales,[2] and Joel B. Sankey[3]

[1]Department of Geosciences, The University of Tulsa, Tulsa, Oklahoma 74104, USA; [2]Department of Earth and Environmental Science, Temple University, Philadelphia, Pennsylvania 19122, USA; [3]Southwest Biological Science Center, Grand Canyon Monitoring and Research Center, US Geological Survey, Flagstaff, Arizona 86001, USA

Abstract

The rapid conversion of grasslands into shrublands has been observed in many arid and semiarid regions worldwide. Studies have shown that fire can negatively affect shrub communities and promote resource homogenization, thereby providing some reversibility to the resource heterogeneity induced by shrub encroachment, especially in the early stages of encroachment. Here, we used prescribed fire in a grassland–shrubland transition zone in the northern Chihuahuan Desert to test the hypothesis that fire facilitates the remobilization of nutrient-enriched soil from shrub microsites to grass and bare microsites and thereby reduces the spatial heterogeneity of soil resources. Results show that the shrub microsites had the lowest water content compared to grass and bare microsites after fire, even when rain events occurred. Significant differences of total soil carbon (TC) and total soil nitrogen (TN) among the three microsites were not detected 1 year after the fire. The spatial autocorrelation distance increased from 1 to 2 m, approximately the mean diameter of an individual shrub canopy, to over 5 m 1 year after the fire for TC and TN. Patches of high soil C and N decomposed 1 year after the prescribed fire. Overall, fire stimulates the redistribution of soil C and N from shrub microsites to nutrient-depleted grass and bare microsites, leading to a decrease in spatial heterogeneity of these elements. The redistribution of soil C and N from shrub to grass and bare microsites, coupled with the reduced soil water content under the shrub canopies but not in grass and bare microsites, suggests that fire might influence the competition between shrubs and grasses, leading to a higher grass, compared to shrub, coverage in this ecotone.

Key words: shrub encroachment; wildfire; spatial heterogeneity; soil redistribution; microsites; geostatistics.

Received 29 September 2017; accepted 6 May 2018;
published online 24 May 2018

Authors' Contributions: GW performed research, analyzed samples, interpreted data, and wrote the paper; JL conceived the study, performed research, and guided paper writing; SR conceived the study and revised the paper; DD performed research; HG performed research; JB designed the experiment and revised the paper.

**Corresponding author; e-mail:* guw647@utulsa.edu

Introduction

Globally, in many arid and semiarid grassland systems, woody plant encroachment has dramatically changed land cover patterns, which has resulted in substantial soil loss and exacerbated desertification (Schlesinger and others 1990; Allred 1996; Van Auken 2000; Gibbens and others 2005; Throop and others 2013; Puttock and others 2014). The erosion and redistribution of soil resources in these regions result in a heterogeneous patchy landscape with hydrologically and nutrient-enhanced vegetated microsites and nutrient-depleted bare soil interspaces, often considered a manifestation of land degradation (Schelsinger and others 1990). On the other hand, recurrent disturbances such as fires are known to decrease vegetation cover and increase soil erodibility (Ravi and others 2007; Sankey and others 2009; Field and others 2011). Although the accelerated soil erosion may contribute to land degradation of some ecosystems (Breshears and others 2003; Sankey and others 2009, 2012b, c; Miller and others 2012; Merino-Martín and others 2014), several studies have also found that periodic fire favors the homogenization of soil resources and can provide some form of reversibility for the grass–shrub transition, especially in the early stages of shrub encroachment (Van Wilgen and Trollope 2003; White and others 2006; Ravi and others 2009; Ravi and D'Odorico 2009; White 2011; Sankey and others 2012a).

Interactions and feedbacks exist among fire, wind erosion, and vegetation in many arid and semiarid lands, and are thought to impact the progression of land degradation (Okin and Gillette 2001; Breshears and others 2003; Ravi and others 2007; Sankey and others 2009, 2012b, c; Field and others 2011; Miller and others 2012; Merino-Martín and others 2014; Ladwig and others 2014). During the shrub encroachment process, when herbaceous plant cover is reduced, accelerated local-scale erosion redistributes soil materials from bare patches to shrub canopy patches, resulting in self-reinforcing ''islands of fertility'' under the canopy of shrubs (Schlesinger and others 1990; Ravi and others 2010). Furthermore, undershrub soil surfaces erode at substantially slower rates than barren interspaces, creating a positive feedback that reinforces the micro-topographic development of raised shrub mounds and lower-elevation interspaces (Breshears and others 2003; D'Odorico and others 2010; Sankey and others 2012b). With the occurrence of fire, most shrub canopies and grasses can be temporarily removed, leading to enhanced wind erosion of the surface materials (White and others 2006; White 2011; Sankey and others 2011, 2012a, c). Furthermore, the volatile organic compounds released by burning vegetation can induce soil water repellency in the vegetated microsites, which can accelerate patch-scale runoff and soil erosion (DeBano 1966, 2000; Ravi and others 2006, 2007; Sankey and others 2012b). In addition, frequent and intense fire act as a dominant control over the survival of woody plant seedlings (D'Odorico and others 2012; Sankey and others 2012b), which are sensitive to fire. Some shrubs are susceptible to fire-induced mortality before reaching a certain growth stage and others may not even resprout after the destruction of aboveground biomass (McPherson 1995; Barger and others 2011).

Owing to fire-induced mortality and top kill of shrubs, residual charred stumps in recently burned landscapes have limited capacity to capture wind-blown sediments or to resist erosion compared to unburned shrubs (Sankey and others 2010). Nevertheless, burned stumps and stems do provide some surface roughness, which results in less erosion, compared to surfaces where the shrubs were completely combusted (Sankey and others 2010). Leaf litter is also lost after fires, which exposes soil surface directly to the erosive action of wind (Neary and others 2005). Moreover, the elevated micro-topographic position makes soil in shrub microsites vulnerable to wind erosion, leading to the erosion of nutrient-enriched soil and ash under the shrub canopies and the redistribution of the associated soil properties (Parsons and others 1992; Ravi and others 2009; Sankey and others 2011; 2012a, b, c). Conversely, microsites with grass, which resprout more quickly than shrubs after fire and have aboveground meristems that are able to capture wind-blown sediments, tend to become the dominant sink areas of wind-blown sediments and nutrients (Ravi and others 2009).

Despite the importance of the interactions among fire, eolian processes, soil nutrients and vegetation in ecosystem degradation, field-based experiments that explicitly link soil nutrient redistribution to post-fire eolian sediment transport in grass–shrub ecotones are still lacking, particularly at the fine spatial scales of vegetation microsites. Studies that specifically focus at the fine scale and on the role of individual plant microsites are required to pinpoint the precise interactions among plants, soil, and external factors. Here, we conducted an experiment in a grassland–shrubland ecotone to investigate the post-fire soil carbon (C) and nitrogen (N) redistribution. Soil C concentration is an important component of and proxy for the amount of organic matter in soils (Schlesinger and Andrews 2000). Soil N is the most important essential macronutrient in desert ecosystems that determines plant growth and can be used as an indicator of desertification (Schlesinger and others 1999; Hartley and others 2007).

The objective of this study was to investigate the variation of total carbon (TC) and total nitrogen (TN) in the surface soil as a result of a prescribed fire at a grass–shrub ecotone, with the particular focus on microsites beneath shrubs and grasses, as well as the bare soil interspaces. Our hypothesis is that fire and the subsequent enhanced wind erosion facilitate the transfer of nutrient-enriched soil from the fertile shrub islands to the nutrient-depleted bare interspaces, thereby reducing the spatial heterogeneity of surface soil and affecting the recovery of vegetation.

Methods

Site Description

The study site is a grass–shrub transition zone located at Sevilleta National Wildlife Refuge (SNWR) in the northern Chihuahuan Desert, 42 km northeast of Socorro, New Mexico, USA. This site is a black grama (*Bouteloua eriopoda*)-dominated grassland with creosote bush shrubs (*Larrea tridentata*), and the soil is primarily sandy loam (Johnson 1988; Cunliffe and others 2016). The field site exhibits a heterogeneous landscape with a mosaic of grasses (55–60% land coverage), shrubs (5–10%), and bare soil interspaces (30–35%) (D'Odorico and others 2010). The relatively sparse grass cover in this transition system provides enough connectivity for fires to spread under ideal burning conditions (Ravi and others 2009; Dukes and others 2018). The windy season is from March to May and the predominant wind is from the southwest (Dukes and others 2018). Most of the summer precipitation occurs from June to September, during the North American Monsoon (Gosz and others 1995; Báez and Collins 2008).

Experimental Methods

In March 2016, we established two 100 m × 100 m monitoring areas (one burned and one control), separated by 250 m and oriented along a line perpendicular to the prevailing wind direction (Figure 1A). These two areas are characterized by similar soil texture, vegetation coverage, and topography. We conducted a prescribed fire in one of the monitoring areas on March 10, 2016, to create the burned treatment (Figure 1B, C). Each of the monitoring areas contains three 30 m × 10 m replicated plots that are oriented with long axis parallel to the predominant wind direction to minimize interactions. In the middle of each 30 m × 10 m plot, a 5 m × 5 m sampling area was established to collect soil samples (Figure 1A).

The treated areas contain three types of microsites, namely grass, shrub, and bare interspace. Grass microsites are areas with grass growth and areas beneath grass canopies. Shrub microsites refer to areas under shrub canopies and commonly range in diameter from 50 to 150 cm. Bare interspace microsites are characterized by soil surface with no visible vegetation coverage and usually lie between neighboring vegetated microsites.

Within each (5 m × 5 m) sampling area, we collected 50 randomly distributed soil samples from the top 5 cm of the soil profile twice a year before and after the spring windy season (Figure 1B–D). The coordinates of the sampling locations were randomly generated, and a different set of sampling locations was used for each sampling period. During the process of soil sampling, locations of the soil samples were carefully determined to an accuracy of 1 cm in the 5 m × 5 m sampling area. The microsite type of every sampling point was also recorded. The three sampling periods were (1) March 2016, immediately after the prescribed fire; (2) June 2016, after one windy season following the prescribed fire; and (3) March 2017, 1 year after the prescribed fire.

Two identical 4-m tall meteorological towers were installed in the burned and control areas. The wind speed was measured every second at 4 different heights (0.5, 1.0, 2.0, and 4.0 m) and averaged with 1-min interval. Soil volumetric water content (VWC) at each type of the microsite was measured using a soil water content reflectometer (CS 655, 12 cm soil water content reflectometer, Campbell Scientific, UT, USA).

Two sets of MWAC (Modified Wilson and Cooke) and one set of BSNE (Big Spring Number Eight) sediment samplers were installed on each plot in order to measure the horizontal mass flux of the eolian transport. The detailed description of the samplers and the calculation of the time-averaged horizontal flux can be seen in Dukes and others (2018).

Plant cover and community composition of each treated area were monitored by two 50-m line intercept transects (parallel and perpendicular to wind direction) every March and June. The plant canopy height and width, as well as the interspace width, were measured along the transects.

Laboratory Analysis

In the laboratory, each soil sample was air-dried and sieved through a 2-mm screen to remove roots, debris, and gravels. Each sample was then ground to fine powder by a ball mill (PBM-04 Planetary Ball Mill, RETSCH, Germany). The content of TC and TN in the soil samples was determined via dry combustion using an element analyzer (FLASH

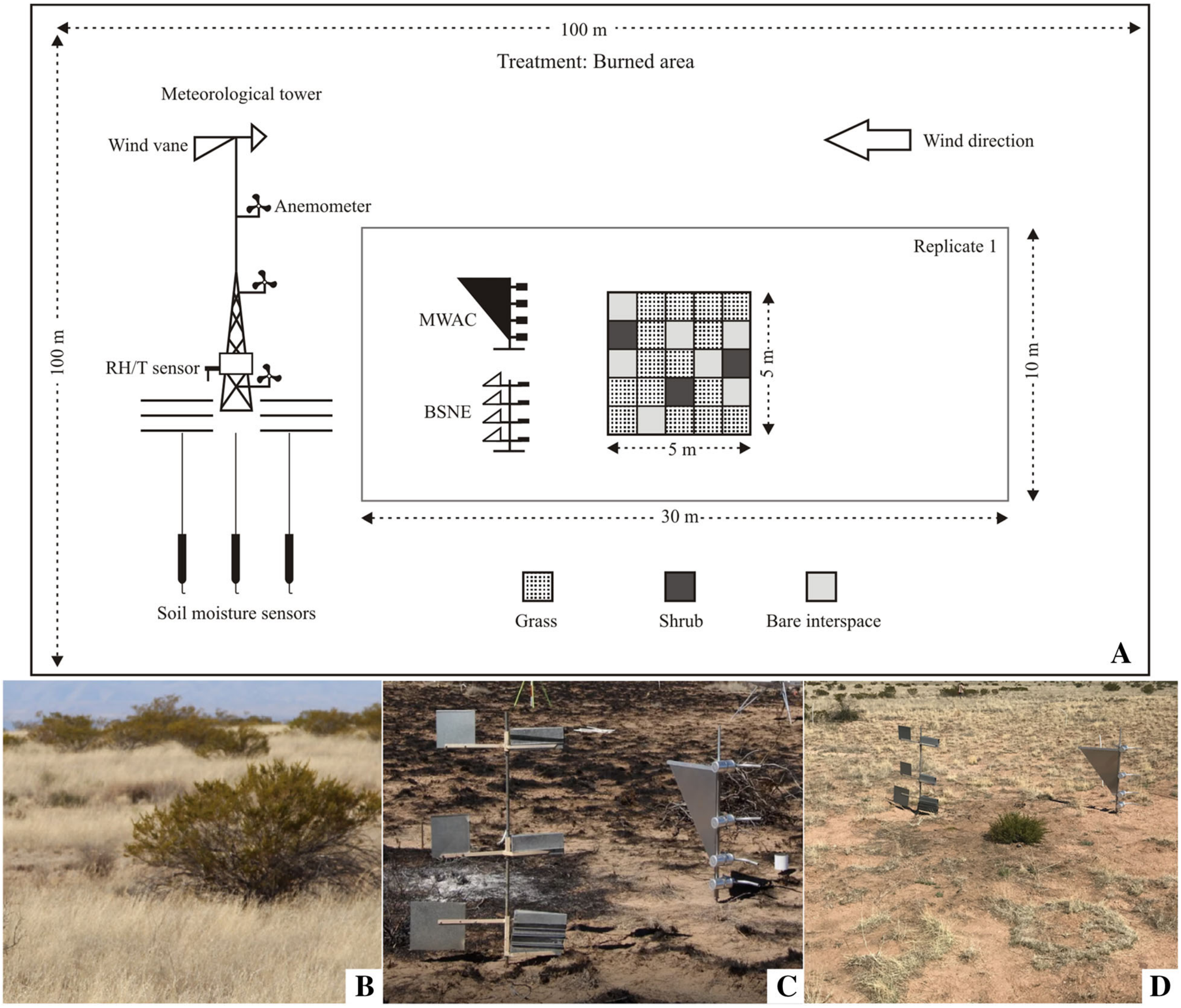

Figure 1. **A** Experimental layout in the field; **B** the surface condition of the study area in Mar. 2016 before the prescribed fire; **C** the surface condition of the control site in Mar. 2016 immediately after the prescribed fire; **D** the surface condition of the burned site in Mar. 2017 (1 year after the prescribed fire). Note diagram **A** was not made to scale.

2000 OEA, Thermal Fisher Scientific, USA). This instrument uses approximately 15 mg of subsamples.

Data Analysis

Conventional Statistical Analysis

For both the burned and control plots, we calculated the mean concentrations of soil TC, TN, C/N ratio for the entire sample ($n = 50$) as well as the mean values of TC, TN, C/N ratio for soil samples collected from different types of microsite (n varies). The coefficient of variation of TC and TN was also calculated to describe the overall variations among samples taken at each sampling plot. The difference of soil TC and TN between the burned and control plots for the entire sample was compared by t-test, and we also conducted one-way ANOVA to compare the mean values of the TC and TN in different sampling periods in the burned and control plots. Finally, a two-way ANOVA was performed to identify the difference of TC and TN among different microsites (factor 1) and different sampling periods (factor 2). Unless otherwise indicated, we set $P < 0.05$ for significance. All the non-geostatistical analyses were performed using *R* software version 3.3.3 (R Development Core Team 2013).

Geostatistical Analysis

The characteristics of the spatial distribution of soil TC and TN were quantified using geostatistical analyses. Semivariograms, which reveal the average variance found in comparisons of samples taken at increasing distance from one another (Schlesinger and others 1996), were constructed for both C and N for each sampling period. All the data variables were transformed using the natural logarithm prior to analysis in order to more closely approximate normal distributions. A semivariogram was constructed using the lag interval of 0.2 m in each 5 m × 5 m sampling plot. The slightly larger lag interval than the minimum sample separation distance was used to better describe the potential change of soil spatial distributions with the continuation of wind erosion (Li and others 2008). Moreover, the grass clumps in the study area are typically 20 cm in diameter or less, so we expected that grassland with little shrub cover would show a higher nugget value than grassland with more shrub cover. When comparing the isotropic and corresponding anisotropic semivariograms at 0°, 45°, 90°, and 135°, we found no significant directional patterns. Therefore, isotropic semivariograms were used in all analyses.

The spherical model is often used to fit the empirical soil resources distribution (Schlesinger and others 1996; Li and others 2008). The formula of the spherical model is:

$$\gamma(h) = C_0 + \frac{1}{2}C\left[\frac{3h}{A_0} - \frac{h^3}{A_0^3}\right] \quad h<A_0$$

$$\gamma(h) = C_0 + C \quad h>A_0,$$

where h is the lag interval, A_0 is the range, C_0 is the nugget variance, and C is the structural variance. The nugget (C_0) is the intercept of the y-axis on the semivariogram and represents the short-range error (Schlesinger and others 1996). The range (A_0) indicates the distance of spatial dependence. The semivariogram of this model first increases and then reaches the sill (C_0+ C). The magnitude of spatial dependence can be illustrated though $C/(C_0+C)$. High $C/(C_0+C)$ values suggest strong spatial autocorrelation, whereas low values imply weak spatial autocorrelation (Jackson and Caldwell 1993; Li and others 2008).

To further illustrate the changes in the spatial distribution of C and N in surface soil of the study areas, we produced kriged maps using the parameters from the semivariogram models. Maps were produced using ordinary kriging method with a block size of 0.1 × 0.1 m^2. The geostatistical analyses were conducted using the GS^+ package (GS^+ version 10, Gamma Design Software, Plainwell, Michigan).

Results

Characteristics of Physical Environment and Vegetation Coverage

During the study period, the highest average daily wind speed was 12.97 m/s, which occurred on May 1, 2016 (Figure 2A). Generally, erosive winds occurred in spring and late fall. The total precipitation from March 2016 to March 2017 was 192 mm in the study area, and many of the rain events occurred from July to September (Figure 2B).

Distinct patterns of VWC were observed under different microsites between the control site and the burned site (Figure 2C, D). At the control site, VWC was generally the highest at the shrub microsites and the lowest at the grass microsites after heavy rains. At the burned site, the shrub microsites consistently had the lowest water content even when it rained, while the bare and grass microsites had similarly higher soil water content throughout the year. At both the burned and control sites, the VWC falling rate for the three types of microsites was similar after individual rain events.

Vegetation transects show that the wind direction has seemingly indiscernible influence on vegetation and bare interspace coverages. From March 2016 to June 2016, the plant coverage recovered to 19.2% at the burned site, 95% of which were grasses. In March 2017, the total plant coverage at the burned site increased to 24.2%, 87% of which were grasses, and the average plant height recovered to 12 cm. At the control site, the total plant coverage was 49% in March 2017, and grasses accounted for 73% of the total vegetation.

Overall Change of Carbon and Nitrogen

Mean soil C content increased significantly from 0.82 to 1.07% in the burned plots over a 1-year period (Figure 3A, one-way ANOVA, $P < 0.05$), and soil C in the burned plots was also significantly higher than that of the control plots in March 2017 (Figure 3A, t-test, $P < 0.05$). A similar, yet slightly weaker pattern was also observed for soil N between the burned and control plots. However, the increase in TN in the surface soil of the burn plots was not significant (Figure 3B).

During the period of the experiment, the overall variation (denoted by coefficient of variation, CV) of TC and TN generally decreased at the burned site (Table 1). A notable decrease in CVs for both TC and TN was observed from March 2016 to March 2017 as a result of the prescribed fire, whereas at the control site, the CVs for both TC and TN in-

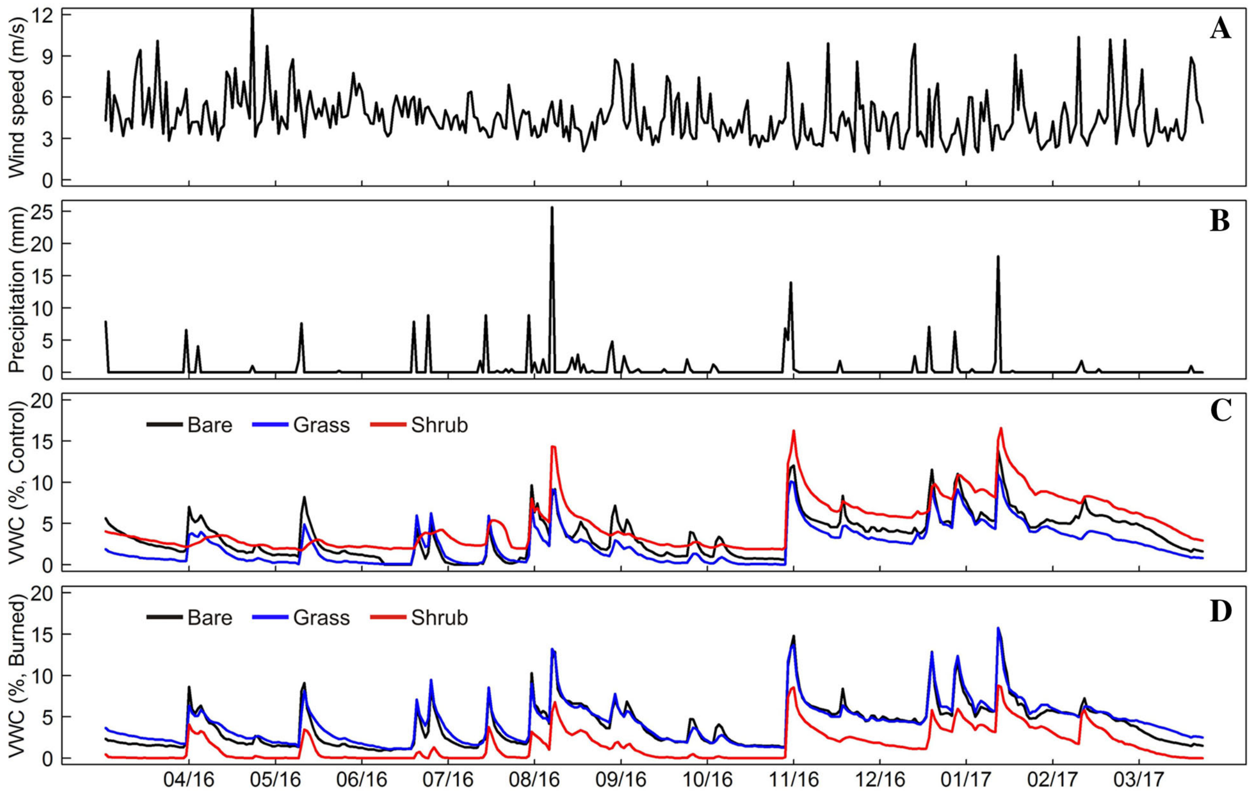

Figure 2. Characteristics of the physical environment of the study site, **A** daily average wind speed (m/s) measured at the height of 4 m, **B** daily precipitation (mm), **C** volumetric water content (VWC, %) under different microsites at the control site, and **D** VWC at the burned site.

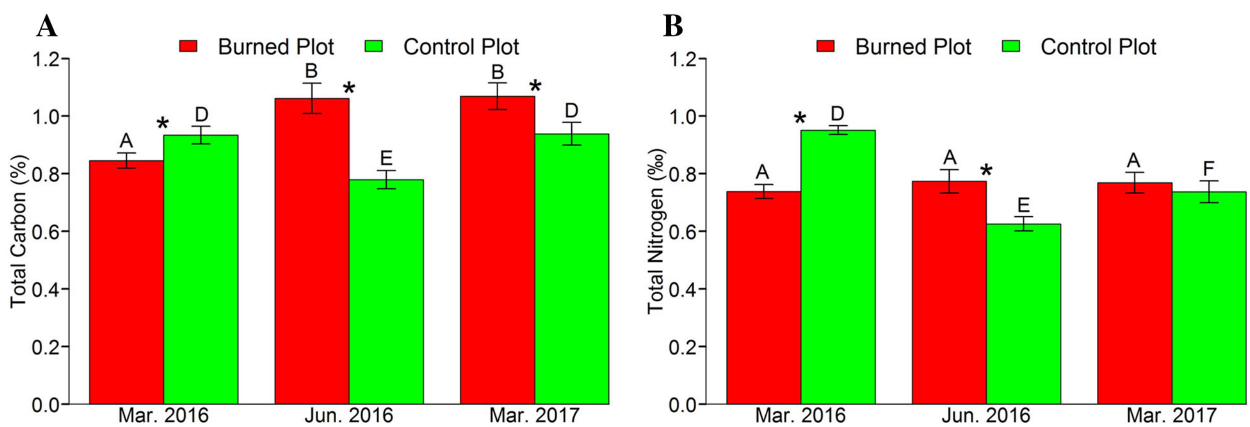

Figure 3. TC and TN of the study areas from March 2016 to March 2017. ''*'' indicates significant difference between burned and control plots for individual sampling periods (*t*-test, $P < 0.05$). Different letters indicate significant difference between the burned or the control plots at different sampling periods (one-way ANOVA, $P < 0.05$).

creased from around 15–40% after one windy season and then remained almost constant till March 2017. Additionally, the average C/N ratios in the burned treatment site increased moderately from 11.89 to 13.78 during the experiment time period.

Change of Carbon and Nitrogen at Different Types of Microsites

At the beginning of the experiment, soil TC under the shrub microsites was significantly greater than both the bare and grass microsites in the burned

Table 1. Coefficient of Variation [(SD/mean) × 100%] for TC and TN, and the C/N Ratios of the Study Areas from March 2016 to March 2017

Treatment	Burned			Control		
Parameter	CV (%)		C/N ratio	CV (%)		C/N ratio
	TC	TN		TC	TN	
Mar. 2016	39	31	11.89	16	15	10.19
Jun. 2016	34	38	13.66	42	40	12.59
Mar. 2017	25	28	13.78	41	40	13.01

n = 50.

plot (Figure 4A). After 1 year in March 2017, no significant difference in soil TC existed among the three types of microsites in the burned plot (Figure 4C). In contrast, soil TC in the shrub microsites was higher than the other two types of microsites in the control plot (Figure 4E, F). Figure 4 also shows that the temporal change of soil C content after the prescribed fire was only minor at different microsites, as no significant change was found in any of the microsites from June 2016 to March 2017.

The variation of soil N at the microsites is similar to that of the soil TC (Figure 5). Although significant differences in TN existed between shrub microsites and the other two microsites initially, TN did not vary significantly among the microsites in March 2017, 1 year after the prescribed fire.

Geostatistical Analysis

Semivariograms and Spatial Autocorrelation

The spherical model provided a good fit to the semivariograms. The range A_0 and spatial dependence index $C/(C_0+C)$ of the semivariogram for TC and TN in each plot throughout the experimental period are presented in Table 2.

Following the prescribed fire in March 2016, soil TC in the burned and control plots was autocorrelated over a distance of 1.83 and 0.95 m, respectively. After the spring windy season, the autocorrelation distance in both the burned and control plots was even shorter. In March 2017, 1 year after the prescribed fire, soil C in the burned plot was autocorrelated at a much larger distance (> 5 m), whereas in the control plot the distance was 2.20 m. During the same period of time, the magnitude of spatial dependence ($C/(C_0+C)$) changed slightly from greater than 90% to about 86% for both the burned and control plots.

In March 2016, the autocorrelation distance for soil TN was 1.60 and 2.71 m for the burned and control plots, respectively. After 1 year, the autocorrelation range for the burned plot increased substantially to greater than 5 m, whereas it decreased to 1.55 m for the control plot. The variance that was spatially dependent ($C/(C_0+C)$) for the burned plot increased from 84 to 99% during the spring windy season and then decreased to 86%. Different from the burned plot, the $C/(C_0+C)$ ratio for TN in the control plot increased after the spring windy season and then remained high in March 2017.

Kriging Analysis

The kriging maps show that soil C and N were patchily distributed in the burned and control plots (Figures 6, 7). This high variation of soil C and N content was also observed in the results of the conventional statistical analyses (Table 1). At the beginning of the study, a strong concentrated area was found for C and N in the burned plot. In June 2016, two relatively smaller patches were observed in the burned plot for both C and N after the spring windy season. In March 2017, 1 year after the prescribed fire, strong patches of C and N disappeared from the burned plot, whereas such strong patches persisted in the control plot. The kriging maps also show that the presence of C and N patches is generally in agreement with the distribution of shrubs. Because of the random sampling scheme, some microsites might not have been sampled when collecting soil samples as well as recording microsite types, resulting in some unexplained spatial and temporal variations in the kriging results.

Discussion

The northern Chihuahuan Desert has experienced extensive encroachment of grasslands by shrubs over the past 150 years (Buffington and Herbel 1965; Gibbens and others 2005; Snyder and Tartowski 2006; Li and others 2007; Okin and others 2009a, b; D'Odorico and others 2012). Although the mechanisms of such a rapid ecosystem change are still under debate, D'Odorico and others (2012) pointed out that the absence of wildfire and only a sporadic use of prescribed fire in rangeland management may provide a positive feedback to the shrub dominance in many semiarid grasslands. It is well known that fire can kill shrub seedlings and thus prevent shrubs from expanding in some landscapes (D'Odorico and others 2012; Okin and others 2009b). However, the role of post-fire wind and water erosion in altering and redistributing

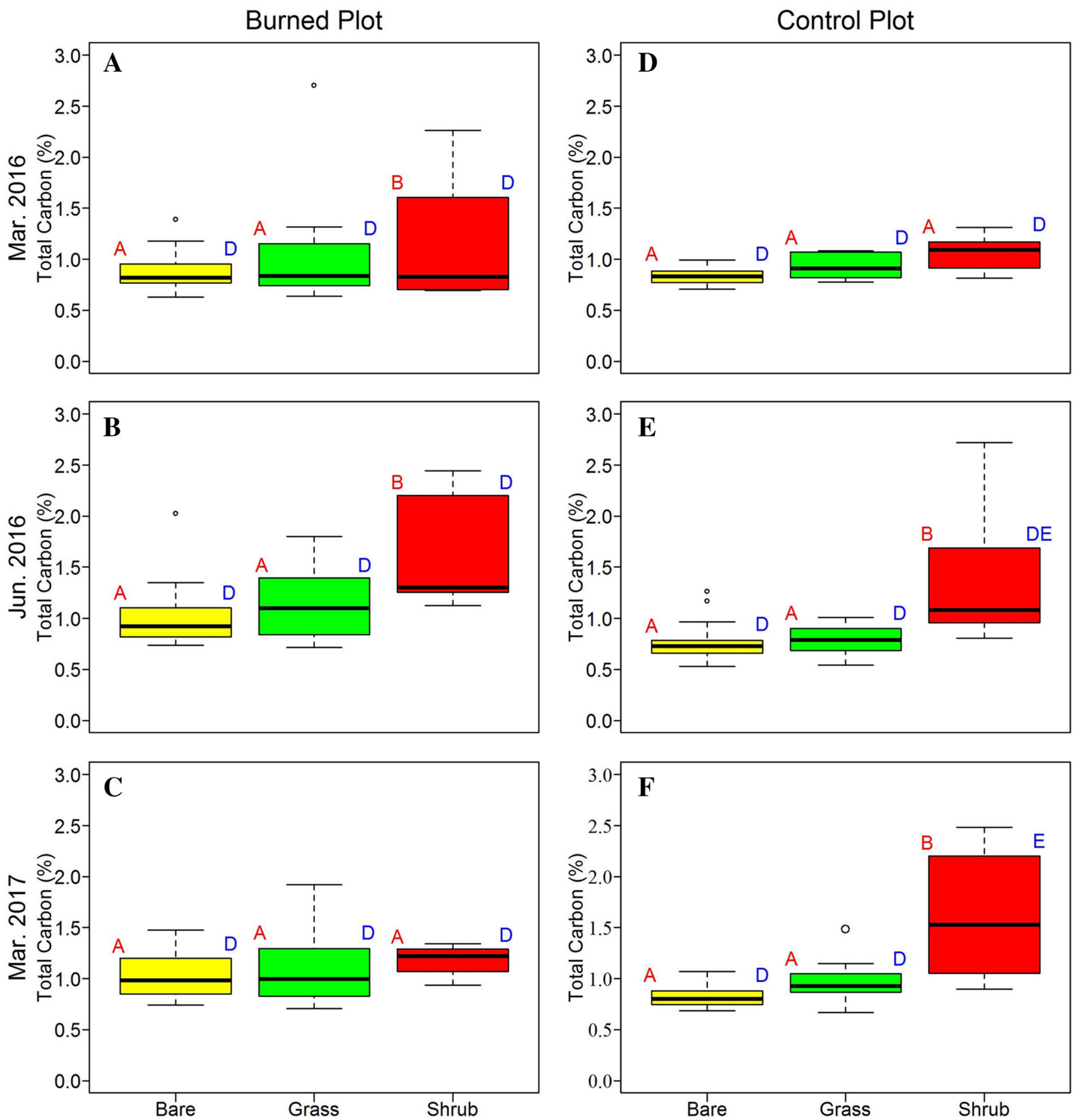

Figure 4. Box plot showing the change of total carbon (TC) content at different microsites in the burned and control plots during the experimental period. A two-way ANOVA was conducted for the burned and control plots separately. The red letters (located on the left side of each box) show the statistical results for bare, grass, and shrub microsites, and the blue letters (located on the right side of each box) indicate the results for the change of individual microsites with different sampling times. Significance is indicated by different letters ($P < 0.05$). Note the horizontal bars in the boxes are medians (Color figure online).

rangeland resources such as soil water, organic matter, and nitrogen is not as well documented in arid and semiarid systems.

Post-fire climatic conditions affect aboveground biomass recovery substantially in semiarid ecosystems (Drewa and others 2006; Burnett and others 2012). Ladwig and others (2014) demonstrated that precipitation could influence community trajectories during post-fire recovery in semiarid regions. Large amounts of precipitation can accelerate plant recovery, whereas drought is likely to delay the regrowth of perennial grasses (Burnett

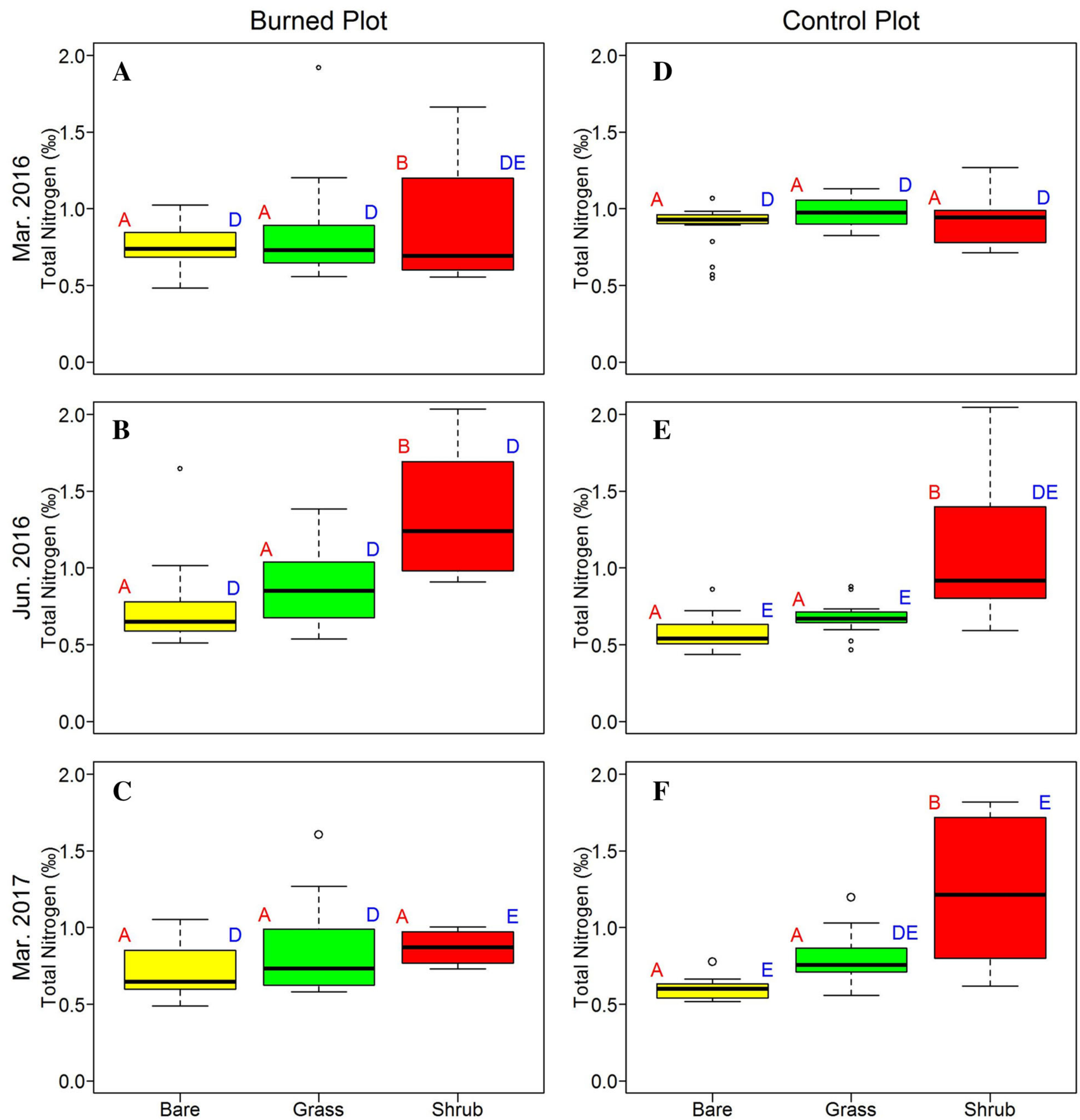

Figure 5. Box plot showing the change of total nitrogen (TN) content at bare, grass, and shrub microsites in the burned and control plots during the experimental period. Details of the statistical analysis and labeling of the results are found in Figure 4.

and others 2012). Results of our study showed that the effect of fire on soil water content varied depending on the microsite types. The shrub microsites were characterized by the lowest soil moisture content post-fire, which in a previous study has been attributed to the post-fire soil hydrophobicity induced by the burning of shrub biomass and surface litter (Ravi and others 2006). This patch-scale soil water repellency–soil erosion feedback is known to decrease water infiltration and increase runoff in the soil surface (Ravi and others 2009). The reduced soil moisture content in shrub microsites may lead to greater surface runoff during intense rain events, which can accelerate the transport of nutrient-rich ash and surface soil aggregates and reduce water retention in the microsites. Such alterations in patch-scale soil and hydrological processes in this ecosystem may even

Table 2. Summary of the Semivariogram Model Parameters for Carbon and Nitrogen Concentrations in Burned and Control Plots During the Experimental Period

Elements	Carbon				Nitrogen			
Time	A_0 (m)		$C/(C_0 + C)$		A_0 (m)		$C/(C_0 + C)$	
	Burned	Control	Burned	Control	Burned	Control	Burned	Control
Mar. 2016	1.83	0.95	0.94	0.95	1.60	2.71	0.84	0.85
Jun. 2016	1.41	0.87	0.98	0.99	1.25	1.12	0.99	0.99
Mar. 2017	> 5.0	2.20	0.89	0.86	> 5.0	1.55	0.86	0.99

diminish the viability of microbes involved in biogeochemical cycling and can prevent the recolonization of new plants (Ice and others 2004).

Reduced soil water content after the fire, however, may affect shrubs and grasses differently. Black grama, a typical C4 grass, inherently has a higher water use efficiency than C3 shrubs, which can improve the competitiveness of grasses over shrubs (West and others 2006; D'Odorico and others 2012). Compared to shrubs, many grasses also respond faster to the post-fire increase in the availability of nitrogen and phosphorus, especially in low-nutrient desert grassland ecosystems (Brooks and Pyke 2001). Moreover, previous studies have demonstrated that herbaceous plants can recover to pre-fire levels within 1–2 years post-fire, while shrubs may need up to 12 years to recover to pre-fire canopy sizes in the Chihuahuan Desert (Parmenter 2008; Sankey and others 2012a). Results of our study also showed that grasses recovered much faster than shrubs after the fire, which might be explained by the combined effect of additional nutrient inputs, increased soil water availability, and different water use efficiency.

The significant change of the spatial distribution patterns of TC and TN after a spring windy season is likely caused by post-fire eolian processes. In the study area, the average horizontal mass flux in the burned plots (75.3 g m^{-1} d^{-1}) was nearly three times higher than in the control plots (27.1 g m^{-1} d^{-1}) (Dukes and others 2018). The decreased CV of TC and TN at the burned site indicates that they were more homogeneously distributed after a windy season. The increased C/N ratio in the burned plots reflects more efficient plant–microbial interactions, as organic matter may experience rapid decomposition after fire (Pauli 1964; Li and others 2007).

Results of our study highlighted the differential changes in the surface soil TC and TN by microsite types after the fire. Although nutrient concentrations were greater in the shrub microsites immediately after the fire, the difference among these microsites decreased with time, and finally became insignificant in March 2017. Such a change in the TC and TN concentrations among different microsites suggests that strong fertility islands that were formed under shrubs before the fire may have disappeared by 1 year after the fire. This assertion was further supported by the geostatistical analysis, which showed that the scale of spatial autocorrelation within the burned site changed from approximately the diameter of an individual shrub canopy to greater than 5 m (Table 2).

Although we did not observe a significant change of TC and TN in the grass microsites (Figure 1C), grasses are known to keep their pedestals with fibrous meristems after fire and therefore can capture wind-blown sediments and protect the sediments in grass microsites from erosion (Lauenroth and others 1993; Neary and others 2005; White 2011; D'Odorico and others 2012). Bare microsites occupy the lowest micro-topographic positions, making them potentially more suitable for sediment deposition and thereby transforming their function from predominant source to possible sink of sediments and nutrients after fire (Sankey and others 2012a).

The kriging maps of geostatistical analysis showed the spatial patterns of TC and TN and their relationships with microsites. The spatial clustering of TC and TN in the control plot are closely related with the fertile islands formed under shrubs, which agrees with many other studies in shrubby grasslands, showing that the patchy distribution of vegetation is normally mirrored in the soil beneath it (for example, Schlesinger and others 1996; Thompson and others 2006; Li and others 2008). The kriging analysis also showed that fire and subsequent enhanced wind erosion have redistributed TC and TN in surface soil with different concentrated zones (denoted by dense contour lines in Figures 6 and 7) after a windy season.

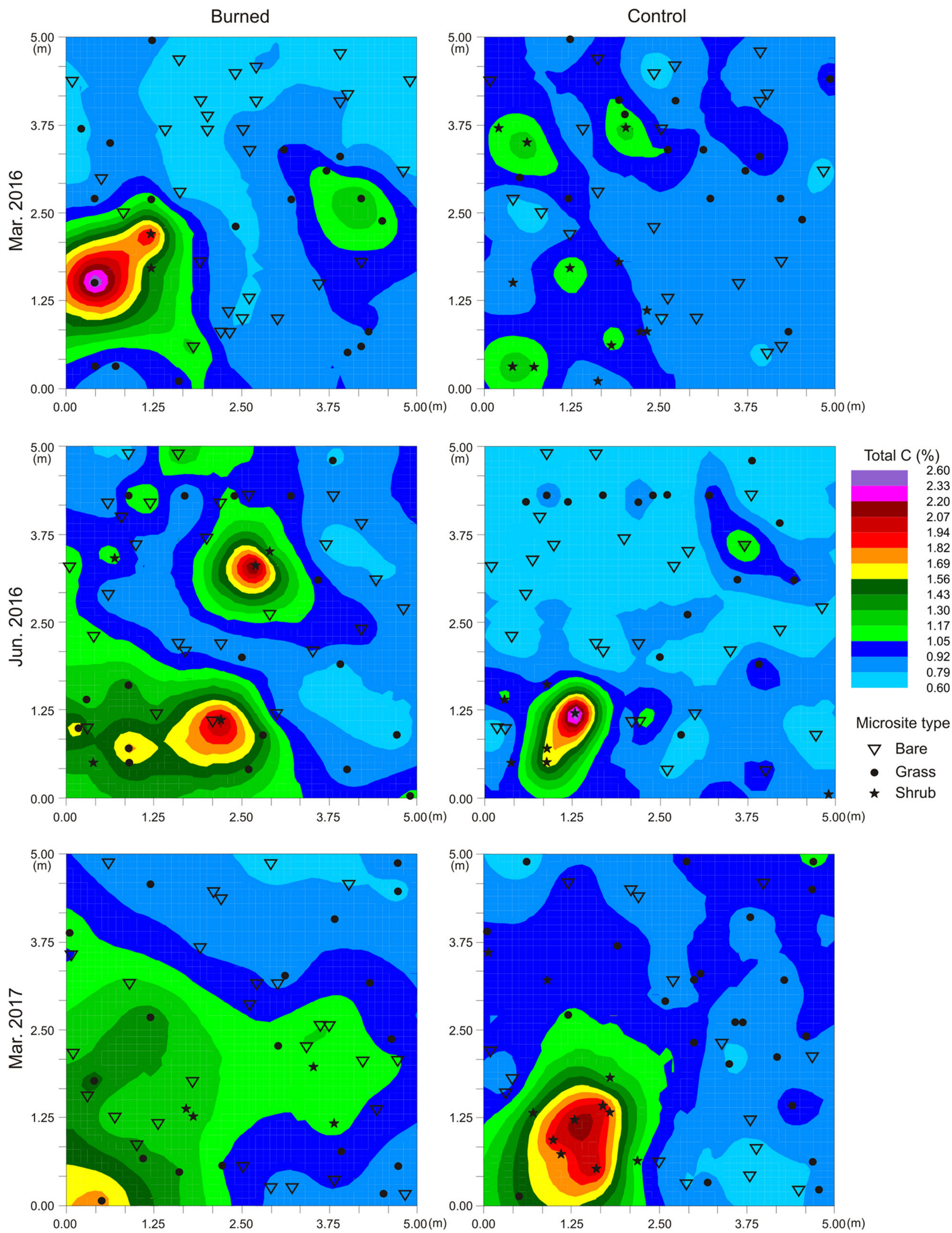

Figure 6. Spatial distribution of soil C concentration (%) predicted by kriging analysis in the 5 m × 5 m sampling area in the burned and control plots.

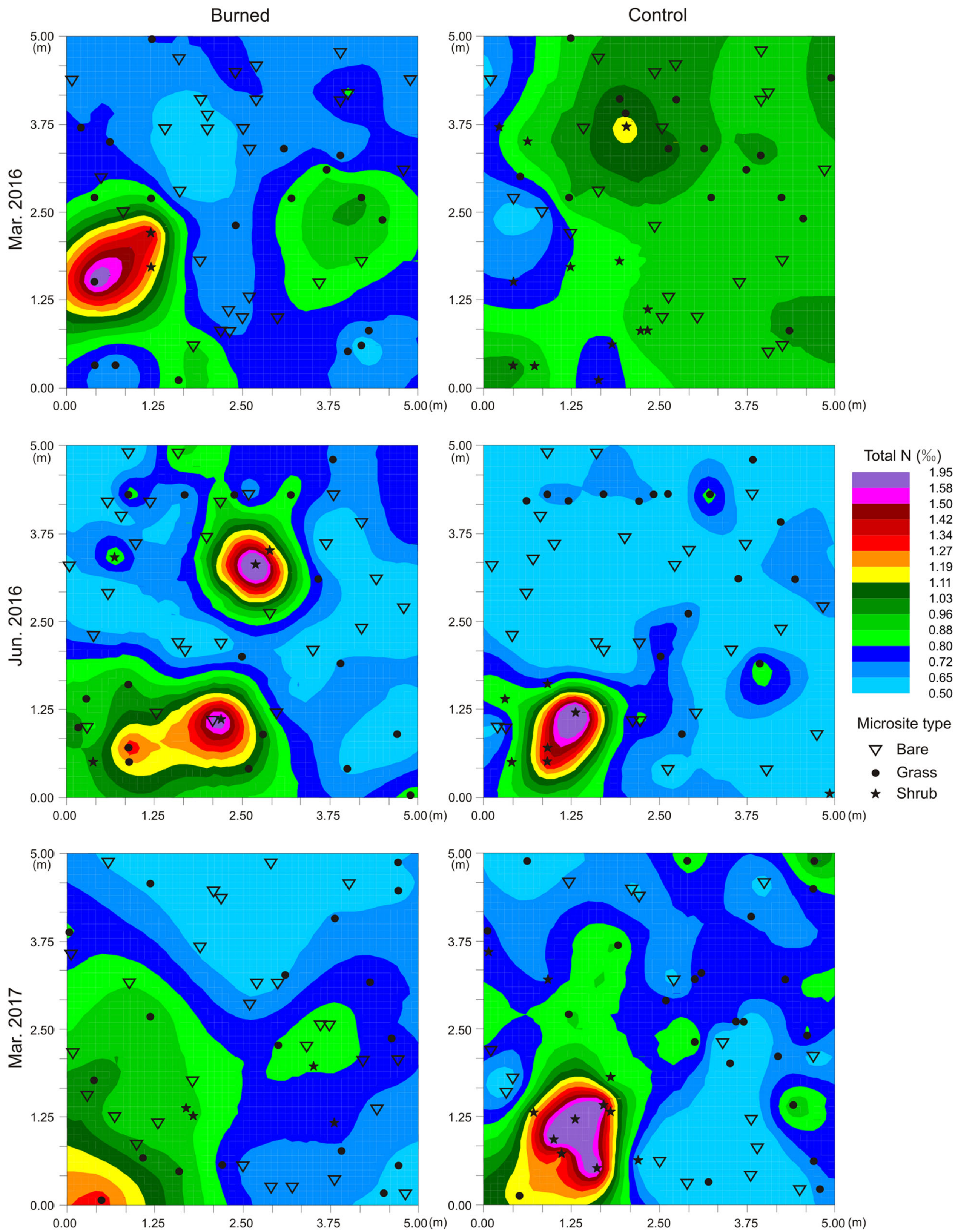

Figure 7. Spatial distribution of soil N concentration (‰) predicted by kriging analysis in the 5 m × 5 m sampling area in the burned and control plots.

However, a much more homogenized surface was observed 1 year later as illustrated by the spatial patterns of soil TC and TN. Without shrub canopies, the shrub microsites lost their advantages in capturing wind- or water-transported sediments derived from uncovered bare interspaces. Combined with the comparably higher micro-topographical relief, shrub microsites transitioned from net soil and nutrient' sinks to source areas, resulting in a disaggregation of the islands of fertility underneath shrub canopies 1-year post-fire. The fibrous surface roots of the grass microsites and the low topographic position of the bare interspaces favor the deposition of wind-blown sediments, leading to the accumulation of nutrient-enriched particles in those microsites. Therefore, the nutrient-rich sediment and ash that were initially stored under shrub canopies tended to be transported to and deposited in grass and bare microsites, leading to more homogeneous soil TC and TN spatial distributions.

Conclusions

Results of our study highlighted the difference between the three types of microsites and elucidated the potential role of fire on counteracting the shrub encroachment process in a grassland–shrubland transition zone in the northern Chihuahuan Desert. The fact that soil moisture was reduced in shrub microsites after the fire, combined with lower water use efficiency of shrubs, suggests that shrubs may lose an important competitive advantage against grasses after burning. Moreover, owing to post-fire shrub mortality, loss of shrub canopies, and raised microtopography, shrub microsites can be transformed from sediment and nutrient sinks to sources following fire. These changes in the soil resources beneath shrubs may further reinforce the newly gained, post-fire competitive advantages of grasses as the dispersion of the nutrient-rich soil aggregates from shrub microsites are deposited on the burned, grass and bare microsites. In our study, the spatial heterogeneity of soil C and N decreased notably 1 year after fire, denoted by the disappearance of the strong islands of fertility associated with shrub microsites. It follows that a more spatially homogeneous distribution of C and N post-fire may promote the establishment of a higher vegetation coverage of grasses than before, thus counteracting the resource heterogeneity induced by the shrub invasion process in this grassland–shrubland transition system.

ACKNOWLEDGEMENTS

This research was supported by the US National Science Foundation Award EAR-1451489 for J. Li and 1451518 for S. Ravi. The authors greatly acknowledge the contributions of Jon Erz, Eric Krueger, and Andy Lopez (FWS, SNWR), Scott Collins and Amaris Swan (Sevilleta LTER, New Mexico, USA), and Bethany Theiling (The University of Tulsa) for providing access to field and laboratory facilities and technical guidance. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government. The data used in the paper can be accessed upon request to the corresponding author (guw647@utulsa.edu).

REFERENCES

Allred KW. 1996. Vegetative changes in New Mexico rangelands. N M J Sci 36:168–231.

Báez S, Collins SL. 2008. Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. PLoS ONE 3(6):e2332.

Barger NN, Archer SR, Campbell JL, Huang CY, Morton JA, Knapp AK. 2011. Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. J Geophys Res Biogeosci. https://doi.org/10.1029/2010JG001506.

Breshears DD, Whicker JJ, Johansen MP, Pinder JE. 2003. Wind and water erosion and transport in semi-arid shrubland, grassland and forest ecosystems: quantifying dominance of horizontal wind-driven transport. Earth Surf Process Landf 28(11):1189–209.

Brooks ML, Pyke DA. 2001. Invasive plants and fire in the deserts of North America. In: Galley KEM, Wilson TP, Eds. Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Fire conference 2000: the first national congress on fire ecology, prevention, and management. Miscellaneous Publication No. 11. Tallahassee, FL: Tall Timbers Research Station. pp 1–14.

Buffington LC, Herbel CH. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecol Monogr 35(2):139–64.

Burnett SA, Hattey JA, Johnson JE, Swann AL, Moore DI, Collins SL. 2012. Effects of fire on belowground biomass in Chihuahuan Desert grassland. Ecosphere 3(11):1–13.

Cunliffe AM, Puttock AK, Turnbull L, Wainwright J, Brazier RE. 2016. Dryland, calcareous soils store (and lose) significant quantities of near-surface organic carbon. J Geophys Res Earth Surf 121(4):684–702.

DeBano LF. 1966. Formation of non-wettable soils involves heat transfer mechanism. In: USDA Forest Service Research Note PSW-132. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. p. 8.

DeBano LF. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. J Hydrol 231:195–206.

D'Odorico P, Fuentes JD, Pockman WT, Collins SL, He Y, Medeiros JS, DeWekker S, Litvak ME. 2010. Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan Desert. Ecosphere 1(6):1–11.

D'Odorico P, Okin GS, Bestelmeyer BT. 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. Ecohydrology 5(5):520–30.

Dukes D, Gonzales HB, Ravi S, Grandstaff DE, Van Pelt RS, Li J, Wang G, Sankey JB. 2018. Quantifying post-fire aeolian sediment transport using rare earth element tracers. J Geophys Res Biogeosci 123:288–99. https://doi.org/10.1002/2017JG004284.

Drewa PB, Peters DP, Havstad KM. 2006. Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert. Oecologia 150(1):29–39.

Field JP, Breshears DD, Whicker JJ, Zou CB. 2011. Interactive effects of grazing and burning on wind- and water-driven sediment fluxes: rangeland management implications. Ecol Appl 21(1):22–32.

Gibbens RP, McNeely RP, Havstad KM, Beck RF, Nolen B. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. J Arid Environ 61(4):651–68.

Gosz JR, Moore DI, Shore GA, Grover GD, Rison W, Rison C. 1995. Lightning estimates of precipitation location and quantity on the Sevilleta LTER, New Mexico. Ecol Appl 5:1141–50.

Hartley A, Barger N, Belnap J, Okin GS. 2007. Dryland ecosystems. In: Marschner P, Rengel Z, Eds. Nutrient cycling in terrestrial ecosystems. Berlin: Springer. p 271–307.

Ice GG, Neary DG, Adams PW. 2004. Effects of wildfire on soils and watershed processes. J For 102(6):16–20.

Jackson RB, Caldwell MM. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. J Ecol 81:683–92.

Johnson WR. 1988. Soil survey of Socorro county area, New Mexico. United States Department of Agriculture, Soil Conservation Service, United States Government Printing Office, Washington, DC.

Lauenroth WK, Urban DL, Coffin DP, Parton WJ, Shugart HH, Kirchner TB, Smith TM. 1993. Modeling vegetation structure-ecosystem process interactions across sites and ecosystems. Ecol Model 67(1):49–80.

Ladwig LM, Collins SL, Ford PL, White LB. 2014. Chihuahuan Desert grassland responds similarly to fall, spring, and summer fires during prolonged drought. Rangel Ecol Manag 67(6):621–8.

Li J, Okin GS, Alvarez L, Epstein H. 2007. Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. Biogeochemistry 85(3):317–32.

Li J, Okin GS, Alvarez L, Epstein H. 2008. Effects of wind erosion on the spatial heterogeneity of soil nutrients in two desert grassland communities. Biogeochemistry 88(1):73–88.

McPherson GR. 1995. The role of fire in desert grasslands. In: Mitchell PM, Thomas RVD, Eds. The desert grassland. Tucson: University of Arizona Press. p 130–51.

Merino-Martín L, Field JP, Villegas JC, Whicker JJ, Breshears DD, Law DJ, Urgeghe AM. 2014. Aeolian sediment and dust fluxes during predominant "background" wind conditions for unburned and burned semiarid grassland: Interplay between particle size and temporal scale. Aeolian Res 14:97–103.

Miller ME, Bowker MA, Reynolds RL, Goldstein HL. 2012. Post-fire land treatments and wind erosion–lessons from the Milford Flat Fire, UT, USA. Aeolian Res 7:29–44.

Neary DG, Ryan KC, DeBano LF. 2005. Wildland fire in ecosystems: effects of fire on soils and water. Gen. Tech. Rep. RMRS-GTR-42-vol 4: 250.

Okin GS, Gillette DA. 2001. Distribution of vegetation in wind-dominated landscapes: implications for wind erosion modeling and landscape processes. J Geophys Res Atmos 106(D9):9673–83.

Okin GS, D'Odorico P, Archer SR. 2009a. Impact of feedbacks on Chihuahuan desert grasslands: transience and metastability. J Geophys Res Biogeosci. https://doi.org/10.1029/2008JG000833.

Okin GS, Parsons AJ, Wainwright J, Herrick JE, Bestelmeyer BT, Peters DC, Fredrickson EL. 2009b. Do changes in connectivity explain desertification? Bioscience 59(3):237–44.

Parmenter RR. 2008. Long-term effects of a summer fire on desert grassland plant demographics in New Mexico. Rangel Ecol Manag 61(2):156–68.

Parsons AJ, Abrahams AD, Simanton JR. 1992. Microtopography and soil-surface materials on semi-arid piedmont hillslopes, southern Arizona. J Arid Environ 22(2):107–15.

Pauli F. 1964. Soil fertility problem in arid and semi-arid lands. Nature 204(4965):1286–8.

Puttock A, Dungait JA, Macleod CJ, Bol R, Brazier RE. 2014. Woody plant encroachment into grasslands leads to accelerated erosion of previously stable organic carbon from dryland soils. J Geophys Res Biogeosci 119(12):2345–57.

R Core Team. 2013. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Ravi S, D'Odorico P, Herbert B, Zobeck T, Over TM. 2006. Enhancement of wind erosion by fire-induced water repellency. Water Resour Res. https://doi.org/10.1029/2006WR004895.

Ravi S, D'Odorico P, Zobeck TM, Over TM, Collins SL. 2007. Feedbacks between fires and wind erosion in heterogeneous arid lands. J Geophys Res Biogeosci. https://doi.org/10.1029/2007JG000474.

Ravi S, D'Odorico P. 2009. Post-fire resource redistribution and fertility island dynamics in shrub encroached desert grasslands: a modeling approach. Landsc Ecol 24(3):325–35.

Ravi S, D'Odorico P, Wang L, White CS, Okin GS, Macko SA, Collins SL. 2009. Post-fire resource redistribution in desert grasslands: a possible negative feedback on land degradation. Ecosystems 12(3):434–44.

Ravi S, Breshears DD, Huxman TE, D'Odorico P. 2010. Land degradation in drylands: interactions among hydrologic–aeolian erosion and vegetation dynamics. Geomorphology 116(3–4):236–245.

Sankey JB, Germino MJ, Glenn NF. 2009. Aeolian sediment transport following wildfire in sagebrush steppe. J Arid Environ 73(10):912–19.

Sankey JB, Glenn NF, Germino MJ, Gironella AIN, Thackray GD. 2010. Relationships of aeolian erosion and deposition with LiDAR-derived landscape surface roughness following wildfire. Geomorphology 119(1):135–45.

Sankey JB, Eitel JU, Glenn NF, Germino MJ, Vierling LA. 2011. Quantifying relationships of burning, roughness, and potential dust emission with laser altimetry of soil surfaces at submeter scales. Geomorphology 135(1):181–90.

Sankey JB, Ravi S, Wallace CS, Webb RH, Huxman TE. 2012a. Quantifying soil surface change in degraded drylands: shrub encroachment and effects of fire and vegetation removal in a desert grassland. J Geophys Res Biogeosci. https://doi.org/10.1029/2012JG002002.

Sankey JB, Germino MJ, Sankey TT, Hoover AN. 2012b. Fire effects on the spatial patterning of soil properties in sagebrush steppe, USA: a meta-analysis. Int J Wildland Fire 21(5):545–56.

Sankey JB, Germino MJ, Glenn NF. 2012c. Dust supply varies with sagebrush microsites and time since burning in experimental erosion events. J Geophys Res Biogeosci. https://doi.org/10.1029/2011JG001724.

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA, Whitford WG. 1990. Biological feedbacks in global desertification. Science (Washington) 247(4946):1043–8.

Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77(2):364–74.

Schlesinger WH, Abrahams AD, Parsons AJ, Wainwright J. 1999. Nutrient losses in runoff from grassland and shrubland habitats in Southern New Mexico: I. Rainfall Simul Exp Biogeochem 45(1):21–34.

Schlesinger WH, Andrews JA. 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48(1):7–20.

Snyder KA, Tartowski SL. 2006. Multi-scale temporal variation in water availability: implications for vegetation dynamics in arid and semi-arid ecosystems. J Arid Environ 65(2):219–34.

Thompson TL, Zaady E, Huancheng P, Wilson TB, Martens DA. 2006. Soil C and N pools in patchy shrublands of the Negev and Chihuahuan Deserts. Soil Biol Biochem 38(7):1943–55.

Throop HL, Lajtha K, Kramer M. 2013. Density fractionation and ^{13}C reveal changes in soil carbon following woody encroachment in a desert ecosystem. Biogeochemistry 112(1–3):409–22.

Van Auken OW. 2000. Shrub invasions of North American semiarid grasslands. Annu Rev Ecol Syst 31(1):197–215.

Van Wilgen B, Trollope W. 2003. Fire as a driver of ecosystem variability. In: Johan TT, Kevin HR, Harry CB, Eds. The Kruger experience: ecology and management of Savanna heterogeneity. Washington, DC: Island Press. p 149–70.

West JB, Bowen GJ, Cerling TE, Ehleringer JR. 2006. Stable isotopes as one of nature's ecological recorders. Trends Ecol Evol 21(7):408–14.

White CS, Pendleton RL, Pendleton BK. 2006. Response of two semiarid grasslands to a second fire application. Rangel Ecol Manag 59(1):98–106.

White CS. 2011. Homogenization of the soil surface following fire in semiarid grasslands. Rangel Ecol Manag 64(4):414–18.